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The Eastern Mediterranean Sea: tropical invasions and niche opportunities in a “Godot Basin”

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SUMMARY

The progressive colonization of large sectors of the Mediterranean Sea by tropical-subtropical alien species (Lessepsian “migrants” and introduced aliens) highlights a remarkable biogeographic paradox. The Eastern Mediterranean Sea, and particularly the Levant basin, shows a capacity of hosting tropical-subtropical benthos elements, a capacity not shared by the rest of the basin. The post-glacial Levant basin is in fact defined a “Godot basin” due to its present oceanographic prerogatives. It has been a potential receptacle of tropical organisms, yet could exploit such potentiality only after casual man induced events. Traditional and more recent niche concepts can be used to better understand the phenomenon of such biological invasions.

Alien species successfully colonize the Godot basin, only when several conditions are favourable. Lower diversity, possibly related to resources not efficiently exploited by autochthonous, offers “niche opportunities” to the newcomers. In the particular case of the Lessepsian invasion, the success probably depends on finding the appropriate time for colonization. This can account for the massive initial invasion and the steady increase of records witnessing a still ongoing process.

INTRODUCTION

From the biogeographer’s perspective the Levant Basin (LB) is a unique laboratory to study one of the most impressive on-going marine colonization observable by man: the Lessepsian invasion (“migrations”, sensu Por, 1971; see also e.g. Por, 1975, 1978, 1990; Por and Dimentman, 1989; Zibrowius, 1991, 1994, Ribera, 1993; Galil, 1993). In fact, wide sectors of the eastern Mediterranean Sea are being invaded by tropical-subtropical species both throughout the Suez

Canal (true Lessepsian invasion) and by accidental introduction by man (Zibrowius, 1991; Boudouresque et al., 1993; CIESM, 2002).

The concept of “Godot basin” was introduced to define a maritime basin with remarkable surface dimensions ($n10^5$ km²), yet complete segregation within a larger basin (mother basin), oceanographic conditions different from those of its host mother basin, inaccessibility to easy floro-faunal invasions by organisms with a thermal tolerance different from that of the mother sea (Taviani, 2002). At present, the Levant Basin possesses all these conditions within the Mediterranean Sea. The Levant Basin has a surface of 667,000 km², is bordered by southern Turkey, Syria, Lebanon, Israel, Egypt, Lybia (partially), and includes Cyprus.

The Eastern Mediterranean as a whole shows an actual capacity of receiving and sustaining shallow-water benthic species with *tropical* or *subtropical* affinity, whilst such capacity is not shared by the rest of the Mediterranean. Furthermore, these newcomers are often capable to form viable, reproductive populations inside the Levant Basin. In short, they show no difficulty to cope with the physico-chemical attributes of present oceanographic conditions in this basin. In fact, one can legitimately expect that migratory events of tropical-subtropical organisms should take place from the eastern Atlantic Senegalese sub-province, both during the present (post-glacial) and previous interglacial times. With only a few known exceptions (the *Strombus* faunas of the last interglaciation), this seems not to have been the case. The possible explanation rests with the difficulty of such organisms to breach through cold waters interposing between the northwest African Atlantic and westernmost Mediterranean basin (Taviani, 2002).

This progressive and inexorable colonization highlights a remarkable biogeographic paradox. The temperate mother basin (Mediterranean, particularly in its western part) acts as a biogeographic barrier for its easternmost Levant sub-basin. The astonishing biogeographic potential of the Levant basin to host tropical-subtropical elements would have been unperceived without the action of man such as accidental introductions and, most of all, the cut of the Suez seaway.

Overall, the success of such invasion implies that the Levant Basin was and still is biologically under-exploited by marine life. In a way this success may indicate that a growing legion of benthic organisms found and is still finding a sort of ecological vacuum where many ecological niches are available. This seems to hold true for coastal marine ecosystems that are the most impacted by the venues of such tropical-subtropical guests.

The aim of this paper is to discuss some unexplored aspects and implications linked to the dynamic re-assessment of the Levantine Basin coastal marine ecosystems under the on-going pressure of benthic tropical-subtropical newcomers. Major questions we want to address are:

- what kind of larval strategy/-ies are favouring such flows?

- what kind of organisms are entering and settling the LB?
- some organisms (parasites, specialized micro-carnivores and browsers) are originally linked to specialized substrata: how do they cope with the absence of their pabulum in the Mediterranean?
- overall, does the success of such invasion imply that the Levant Basin was biologically largely underexploited? Is this a sort of pending ecological niche availability?

DISCUSSION

We stress here that some distinctions should be done between species accidentally introduced by man, like e.g. the gastropods *Strombus persicus* Swainson and *Rapana venosa* (Valenciennes) and true lessepsian migrants, like *Rapana rapiformis* Born. These distinctions have several biological implications (Oliverio, 1995; Chemello and Oliverio, 2001). Keeping this in mind, for the present aims both categories will be considered. The tropical-subtropical benthic invaders belong to various plant and animal phyla among which molluscs possibly represent the best tracer to tackle with the interrogatives above mentioned since they are: (1) quantitatively the largest group, (2) equipped with a shell often keeping memory of developmental and dispersal strategies, (3) adapted to a vast array of ecological functions (including parasitism and other specialized feeding). Nearly 100 mollusc species are recorded in the last published checklist (CIESM, 2000); yet the trend in the publication of new records indicates that the figure will significantly increase (see e.g. Barash and Danin, 1972 Buzzurro and Greppi, 1996).

With the exception of nektonic and holopelagic organisms, larval stages are mostly involved in the Lessepsian “migrations”, yet they are not always (nor necessarily) the vehicle of introductions. One would expect that larval planktotrophy, with its comparably longer planktonic phase, be favoured over lecithotrophy at least in the “migrations”. Chemello and Oliverio (2001) analysed habitat, larval development and substrate requirement of 64 gastropod Lessepsian species. Larval planktotrophy (only 33%) seemed severely counter-selected vs. lecithotrophy (~60%). This was particularly true when considering that Lessepsians originate from an area where planktotrophy is the largely dominant strategy. Results also indicated that only 28% of the species (mostly with planktotrophic larval development) originated from hard bottoms. Added to the prevalence of lecithotrophic developers it was interpreted (see also Safrieli and Lipkin, 1974) as the effect of the lack of hard bottoms and the presence of some constraints against larval planktotrophs along large tracts of the Suez Canal.

The chance of colonising new areas is an opportunity for the species involved in both processes (Lessepsians and introduced) to implement adaptive

potentialities. It was expected that the newcomers be represented at least for the majority, by euryecious elements. Rather surprisingly, a large number of species (33%) was represented by epizoic taxa (ectoparasites to grazers of sponges, annelids, echinoderms and other molluscs). The percentage remains high (~30%) if we include all 31 alien species of the Levant basin (Tab. I).

Our third question (how do specialised organisms cope with the absence of their pabulum in the Mediterranean Sea?) receives only a partial answer since the very few experimental data available. The single Eulimidae has been found living on a Mediterranean cidaroid sea-urchin. A pyramidellid was observed while feeding on the Mediterranean cockle (*Cerastoderma glaucum*). Most of the opisthobranchs were recorded associated with autochthonous targets (sponges, cnidarians, bryozoans, tunicates). On the other hand the most successful group is undoubtedly represented by the least specialised Pyramidellidae.

As already suggested (Oliverio, 1994), traditional niche compression/expansion models can help explain the observed phenomena (Pulliam, 1986; Tilman, 1987; Leibold, 1995). More recent niche concepts can be applied in this case to better understand the phenomenon of the biological invasions. It is widely accepted that high “niche opportunities” (thus, low invasion resistance) result from low species diversity (Shea and Chesson, 2002). The Levant basin is in fact characterised by a significantly reduced diversity compared to the rest of the Mediterranean Sea. Admittedly, lower diversity may be related to resources not being exploited efficiently due to the absence of species with suitable capacities (the “empty niche” or “vacant niche” hypothesis: see Holmes and Price, 1986, and Simberloff, 1995). Thus, only species able to benefit from resources in those particular circumstances will face “niche opportunities”. This could be the case of the two columbellid gastropods of the genus *Zafra*, commonly and abundantly occurring at different depth in the *Posidonia* meadows of southern Turkey. It has been suggested (Shea and Chesson, 2002; and see also Smith and Skúlason, 1996; Stachowicz et al. 1999) that for these events it is the set of functional differences of the autochthonous species’ niches along with their variation in time that trigger the invasion resistance level. All these models deal with occasional introductions of alien species, and can account for the invasion success by the introduced aliens. In the case of the Lessepsian invasion, the continuous influx of larvae from the Red Sea provides the colonisers the possibility of repeatedly attempting a successful competition with autochthonous. Niches can be only partly vacant and invader success depends on finding the appropriate time for colonization. This can account for the massive initial invasion and the steady increase of records in the last 30 years or so, witnessing for a still ongoing process.

Tab. I - Epizoic alien gastropods in the Levant basin. Faunal list from CIESM (2000) modified.

Family	no of species	host/target	specificity in IP
Triphoridae	1	Porifera	***
Cerithiopsidae	2	Porifera	***
Eulimidae	1	Echinodermata	****
Hipponicidae	1	Mollusca	*
Epitoniidae	1	Cnidaria	*****
Pyramidellidae	13	Polychaeta/Mollusca	**
Cimidae	1	Mollusca	**
Pleurobranchidae	1	Tunicata	****
Polyceridae	2	Bryozoa	****
Triophidae	1	Bryozoa	****
Chromodorididae	2	Porifera	****
Dendrodorididae	1	Porifera	****
Tergipedidae	1	Cnidaria	****
Flabellinidae	1	Cnidaria	****
Glaucidae	1	Cnidaria	****
Aeolidioidea	1	Cnidaria	****

A series of issues remains totally unexplored, particularly those related with the genetics of the invaders. Which are the genetic links between the aboriginal populations and the Mediterranean colonisers? Lessepsians are genetically different from introduced species, a continuous input of individuals from the Red Sea being probably the rule for most of them. A consequent, unidirectional, but persistent gene flow is expected from the original populations toward the ones newly established in the Mediterranean. Is the gene flow continuous for all species? Or is it in some instance occasional, ephemeral or even lost? The species introduced usually spread from a few (or very few) individuals, imported at once. Strong founder effects should be the natural consequence in this case. It can easily be expected that - given enough time and - introduced aliens populations might genetically diverge from the aboriginal populations; the fate of alien populations kept under a continuous larval supply in the present oceanographic conditions is certainly more complex. In both cases genetic surveys are urged.

Newcomers exploiting the Mediterranean resources in the Levant Basin have successfully faced the present conditions of the Godot basin. On the other hand, our planet is cyclically experiencing severe and somehow dramatic changes, mostly climatically driven, and the Mediterranean Sea is not exception. How will newcomers react to the short- and mid-term variation of the Mediterranean oceanography, particularly the Levantine basin? Are we able to predict the changes that the Levant basin is going to undergo, and how such changes will feature the Godot basin of the future? At a longer temporal scale, it is predictable that such tropical elements or their descendants will have to face the potentially lethal impact of another astronomically-driven climatic cooling of the Mediterranean basin.

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